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Winter CO_2 fluxes in a sub-alpine grassland in relation to snow cover, radiation and temperature

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Abstract Carbon dioxide (CO_2) emissions were measured over a period of 3 years at the sub-alpine Swiss CARBOMONT site Rigi Seebodenalp. Here we show, that winter respiration contributes larger than expected to the annual CO_2 budget at this high altitude, rich in belowground organic carbon grassland (7–15% C by mass). Furthermore the contribution of winter emissions to the annual CO_2 budget is highly dependent on the definition of "winter" itself. Cumulative winter respiration determined over a 6 month period from 15th of October until 15th of April contributed 23.3 ± 2.4 and 6.0 ± 0.3% to the annual respiration during the years under observation, respectively. The insulation effect of snow and a lowering of the freezing point caused by high concentrations of soil organic solutes prevented the soil from freezing. These conditions favored higher soil temperatures resulting in relatively high respiratory losses. The duration of snow cover and micrometeorological conditions determining the photosynthetic activity of the vegetation during snow-free periods influenced the size and the variability of the winter CO_2 fluxes. Seasonal values are strongly influenced by the days at the end and the beginning of the defined winter period, caused by large variations in length of periods with air temperatures below freezing. Losses of CO_2 from the snow-covered soil were highest in winter 2003/2004. These high losses were partially explained by higher temperatures in the topsoil, caused by higher air temperatures just before snowfall. Thus, losses are not a consequence of higher soil temperatures registered during the summer heat wave 2003. However, water stress in summer 2003 might have caused an increment in dead organic matter in the soil providing additional substrate for microbial respiration in the following winter. Although considerable day-to-day fluctuations in snow effluxes were recorded, no conclusive and generally valid relationship could be found between CO_2 losses from the snow pack and snow depth, rate of snow melt, wind speed or air pressure. This suggests that time lags and hysteresis effects may be more important for understanding winter respiration than concurrent environmental conditions in most ecosystems of comparable type.

Keywords Cold season respiration · Eddy covariance · Pastoral grazing ecosystems · Mountain regions · CARBOMONT · Snow efflux · Heat-wave 2003

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Introduction

Identifying the terrestrial sources and sinks of carbon dioxide (CO_2) has been the focus of considerable research over the last decades, particularly within global observation networks such as FLUXNET (Baldocchi et al. 2001; Baldocchi 2008). Only a small fraction of these studies, however, have focused on quantifying non-growing season fluxes from seasonally snow-covered systems (Brooks et al. 1997; Gilmanov et al. 2004; Wang et al. 2011; Liptzin et al. 2009), although it is expected that these so-called winter fluxes can contribute a significant component to the annual carbon budget of ecosystems (Brooks et al. 1997; Bubier et al. 2002; Oechel et al. 1997).

Fluxes of CO_2 measured during the growing season provide important information on carbon exchange processes and are well known to be the major contributor for annual C balances. Furthermore, it has been shown for forest ecosystems that CO_2 fluxes are largely influenced by extreme events, e.g. the European heat-wave in 2003 (Ciais et al. 2005). In contrast, such a clear response to the European 2003 heat-wave has not been reported for grassland ecosystems yet (Wohlfahrt 2008) and hence fluxes from outside the growing season may actually be more critically affecting the annual C budgets of grasslands.

There is general consensus that respiratory losses during the cold period may offset the carbon budget measured during the growing season (Aurela et al. 2004; Brooks et al. 2004; Kelley et al. 1968; Lafleur et al. 2001; Oechel et al. 1997; Schimel et al. 2002) in any year, not only in years characterized by extreme events. Cold season respiration rates were already measured when first ecosystem CO_2 flux quantification attempts were started (Johnson and Kelley 1970; Kelley et al. 1968; Vourlitis and Oechel 1999; Zimov et al. 1993). To date, only a limited number of CO_2 flux measurements during the winter have been conducted in northern latitude grasslands, as reviewed by Gilmanov et al. (2004) and recently pointed out in a synthesis study across a variety of ecosystems by Wang et al. (2011). Schimel and Clein (1996) found that wintertime ecosystem respiration in the Western U.S. Mountains can account for carbon losses that total half of the growing season net carbon sequestration, with soil emissions representing a large fraction of this lost carbon. The quantification of winter CO_2 effluxes can thus change both the magnitude and the sign of the annual carbon budget.

CO_2 exchange measurements have especially been made during the last two decades in high latitude and high altitude regions (Merbold et al. 2009; Zeeman et al. 2010; Zhuang et al. 2006), since these ecosystems are particularly vulnerable to climate change (IPCC 2007), contain large soil C stocks (Zimov et al. 2006) and are therefore of special interest for quantifying the global terrestrial CO_2 budget. However, most annual estimates of these ecosystems are still only based on summer CO_2 fluxes (Merbold et al. 2009; Kutzbach et al. 2007; Jones et al. 1998; Oechel et al. 1993).

Environmental conditions, such as rain- and snowfall, snow cover, air- and soil temperatures, wind speed and air pressure play an important role in winter CO_2 exchange (Bubier et al. 2002; Mariko et al. 2000; Welker et al. 2000) and can vary significantly among years. Bubier et al. (2002) discussed the physical factors and biological processes influenced by snow cover. Heterotrophic respiration in the soil appears to be active even under snow cover, releasing significant amounts of CO_2 (Kelley et al. 1968; Zimov et al. 1993; Oechel et al. 1997; Brooks et al. 2004). Via its function as a thermally isolating ground cover, snow may significantly decrease the depth to which soil freezes, and may even prevent complete freezing in areas without permafrost, thereby increasing the temperature of the active soil layer during winter (Mariko et al. 2000; Swanson et al. 2005). These favorable soil temperatures, with a critical threshold for active respiration around -7 to -5°C, corresponding to the presence or absence of unfrozen water (Brooks et al. 1997; Osterkamp and Romanovsky 1997) allow significant CO_2 production through a continuation of metabolic activity of soil microorganisms with enzymatic systems that are efficient at low temperatures (Panikov and Dedysh 2000). Additionally, root respiration may contribute to the winter CO_2 emissions (Grogan et al. 2001; Welker et al. 2000).

So far no universal relationship between snow pack characteristics and ecosystem respiration has been established. Some authors report on a clear positive effect of snow pack on CO_2 efflux (Gilmanov et al. 2004; Hardy et al. 2001), whereas others were unable to determine an effect of snow cover on respiration (Jones et al. 1999). Of those who identified possible effects of snow cover the processes governing these

effects seemed to be rather specific and not universal. Bubier et al. (2002) found a good correlation between decreasing atmospheric pressure and increasing winter CO_2 efflux; and Kelley et al. (1968) demonstrated a positive effect of wind speed on CO_2 efflux, because accumulated CO_2 within the snow pack is more rapidly released under conditions of high wind speed than under calm conditions. Liptzin et al. (2009) proposed a combination of the previously found relationships, highlighting four different zones of CO_2 emissions driven with increases in, and duration of snow cover: (1) pulses from freeze–thaw processes; (2) CO_2 emissions, which are related to temperature and (3) moisture; and (4) CO_2 emissions influenced by carbon availability. Given this large variability of findings, our study contributes to the overarching goal to increase our mechanistic understanding of how snow cover and snow-related processes govern winter CO_2 fluxes from grassland ecosystems.

Several studies in the arctic tundra calculated CO_2 fluxes using the diffusion gradient of CO_2 concentrations measured at different depths within the snow pack and at the snow–air interface (Brooks et al. 2004; Kelley et al. 1968; Sommerfeld et al. 1996; Swanson et al. 2005). Other studies used automatic chambers (Christensen et al. 2000; Fahnestock et al. 1999; Panikov and Dedysh 2000; Zimov et al. 1993) or the Bowen ratio energy balance technique (Frank and Dugas 2001) to quantify winter CO_2 emissions. Most field studies employed discrete sampling every few days and hence did not collect continuous flux measurements that are necessary to assess the importance of short-term variations of the CO_2 flux from snow-covered ecosystems over the entire cold season. Only very recently a few micrometeorological studies have started to quantify winter net ecosystems exchange using continuous CO_2-flux data (Aurela et al. 2009; Flanagan et al. 2002; Lafleur and Humphreys 2008; Li et al. 2005; Vourlitis and Oechel 1999).

Here we report on continuous eddy covariance (EC) flux measurements carried out during 3 years including the winter periods. Measurements were taken at the Swiss CARBOMONT (Cernusca et al. 2008) site Rigi Seebodenalp, which is snow covered for about 30% of the year. The objectives of this paper are: (1) to quantify the winter CO_2 fluxes measured during the three winter periods; (2) to evaluate the contribution of the winter CO_2 fluxes to the annual carbon budget of this grassland ecosystem; (3) to investigate the micrometeorological processes controlling winter CO_2 fluxes; and (4) to investigate the temporal evolution of CO_2 fluxes shortly after snow melt.

We hypothesize that the winter derived CO_2 efflux contributes significantly to the site's annual C balance, and that winter respiration is primarily governed by micrometeorological variables such as temperature and wind speed amongst others, since we do not expect a substrate limitation of CO_2 production due to the high organic carbon content in the soil. Additionally, we hypothesize that there must be a continuous loss of CO_2 from the ecosystem to the atmosphere, without distinct peaks at the beginning and the end of the winter season, because soils below the snow cover on grounds without permafrost remain unfrozen all winter.

Methods and site description

Site description

The Rigi Seebodenalp flux site was established in May 2002 as part of the European Union (EU) funded Framework Program 5 project CARBOMONT. The study area, defined as a sub-alpine grassland, is located on a flat shoulder terrace on the north slope of Mount Rigi (47°03′30.0″N, 8°27′26.5″E) in Central Switzerland at an altitude of 1,025 m above sea level (Rogiers et al. 2005, 2008). The site encompasses 32 ha of relatively flat terrain (Fig. 1). Summer land-use is dominated by extensively grazed pastures and meadows (Rogiers et al. 2005). The current terrain is the bottom of a pre-historic vanished lake, which was fed by melt water at the end of the last glaciation (Vogel and Hantke 1989).

Soil carbon content and vegetation composition

A thick sedge peat layer is found on top of the clay-rich lake sediments. The soils have a very high organic carbon content in the topmost 24 cm ranging between 7.2 ± 0.2 and $15.7 \pm 0.9\%$ by mass and are characterized either as stagnic cambisols or folic (drystic) histosols depending on meso-topographic conditions (Müller 2004; Rogiers et al. 2008). The vegetation type is a *Lolium-*

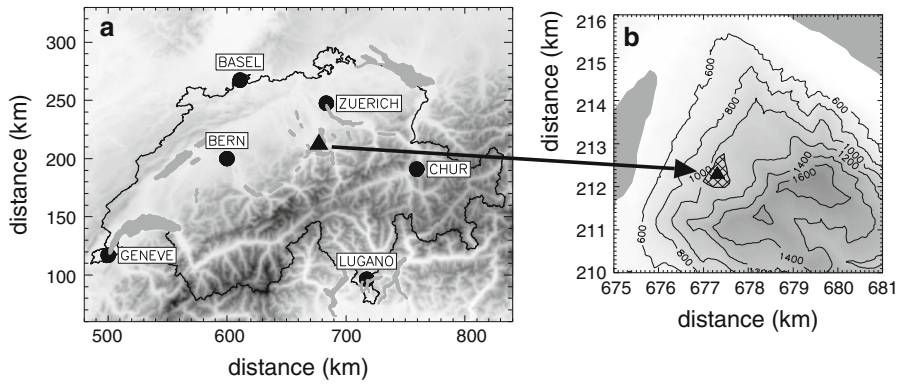

Fig. 1 Map of Switzerland with indication of the CARBOMONT site Seebodenalp (**a**). Topography of the northern part of mount Rigi, the position of the Seebodenalp and the measurement tower are shown (**b**) on a 25-km grid. The maps are in Swiss km-coordinates (DHM25 reproduced with permission, Swisstopo BA046078)

Cynosuretum cristati (rye grass-crested dog's tail) grassland composed of 21–24 vascular plant species with high abundance of *Lolium perenne* L. (rye grass), *Poa pratensis* L. (meadow grass), *Phleum pretense* L. (timothy), *Cerastium holosteoides* Fr. (mouse ear) and *Rumex obustifolius* L. (bitter dock), but relatively low abundance of *Cynosurus cristatus* L. (crested dog's tail) (Reutlinger 2004). In spring *Ranunculus ficaria* L. (pilewort) and *Anthoxanthum odoratum* L. (scented vernal grass) play an important role (Reutlinger 2004).

Flux measurements

The EC technique was used for continuous measurements of the turbulent fluxes of CO_2, water vapor, sensible heat and momentum (see Aubinet et al. 2000; Baldocchi and Bowling 2003, for methodological details). Wind velocity, wind direction, and temperature fluctuations were measured with a three-dimensional ultrasonic anemometer (Solent HS, Gill Ltd., Lymington, UK), mounted at a height of 2.4 m above ground level (a.g.l.). CO_2 and water vapor concentrations were measured with an open-path infrared gas analyzer (LI-7500, LI-COR Inc., Lincoln, Nebraska, USA). Both instruments were sampled at a resolution of 20 Hz. Data processing and treatment followed CarboEurope standards (Mauder et al. 2008) with site-specific details described in Rogiers et al. (2008). In brief, the vertical turbulent fluxes (F) were calculated from the half-hourly averaged covariance of the measured fluctuations of the vertical wind velocity (w, m s^{-1}) in a coordinate system which was aligned with the mean streamlines (McMillen 1988) and the CO_2 concentration (c, µmol):

$$F = \overline{w'c'} \quad (\mu\text{mol m}^{-2}\ \text{s}^{-1}) \tag{1}$$

Overbars denote time averages and primed quantities are the instantaneous deviations from their respective time average. The linear trend in CO_2 concentration was subtracted from each half hour interval to obtain c'. CO_2 fluxes were corrected for high-frequency damping losses (Eugster and Senn 1995) using a damping constant of 0.2 s^{-1}, followed by the necessary density flux correction for open-path instruments according to Webb et al. (1980) and a correction for self-heating of the instrument (the "Burba" correction in a variant suitable for the Rigi Seebodenalp site as described by Rogiers et al. 2008).

Micrometeorological data

To characterize climatic conditions additional meteorological sensors were installed near the EC tower on a separate tower. Air and soil temperatures (°C) were measured with copper-constantan thermocouples at the heights 100, 50, 10, 5 cm aboveground and at −5, −10, −20, −30, −50 cm belowground, measured from the soil surface. Soil moisture data were available for the growing season only, caused by regular sensor failure. Wind speed was measured with a switching anemometer (Vector Instruments, UK) at 2 m height (m s^{-1}). All data were recorded with a data logger (model CR10X, Campbell Scientific Inc., Loughborough, UK).

Snowfall and snow depth were measured manually on a daily basis using a graduated measuring rod at the nearby station Oberiberg at similar altitude (1,090 m a.s.l.) and exposition (north), 6.2 km southeast from Rigi Seebodenalp. The quantitative Oberiberg snow data correspond well with the qualitative information

on snow cover provided by local people from Seebodenalp.

Data availability and post-processing

The EC tower and the micrometeorological station were continuously operated from 17th May 2002 until 10th May 2005, including the three winter periods. Due to some technical failures of the EC system, the data availability before filtering amounted to 88% of all possible 30-min time periods. The data were screened for outliers based on a set of testable plausibility criteria as described in Rogiers et al. (2005). This led to rejection of 7% of available data due to snow- and rainfall and 32% of the data were discarded due to inadequate turbulence conditions, which occurred mainly (65% of these cases) at night (photosynthetic photon flux density ($PPFD$) < 10 μmol m^{-2} s^{-1}). The coverage of high quality data during the three winter periods thus was 61%.

Calculations

CO_2 fluxes were calculated as 30-min averages (Eq. 1) for a 3-year period from May 2002 to May 2005. The annual CO_2 integrals for the 3 years of measurement were obtained by integrating the CO_2 flux data from 15th May until 14th May of the following year. The winter period—or cold season—in this paper was defined as the period from 15th October until 15th April, covering all days when snow blanketed the site in any of the 3 years. This period is longer than the conventional definition of winter but essential due to the long time interval when the study site is covered with snow. The only exceptions were very few anomalous single-day snow events in autumn and spring. It is to be noted that in the Alps at this altitude snow events can occasionally even happen during the warm season. Therefore, our choice of the definition of winter differs from the arbitrary definition of winter in climatology (December–February), but it was not possible to restrict our analysis to December–February, since this would have left too many days with snow cover in the wrong season.

Net ecosystem exchange (NEE) was partitioned into gross primary production (GPP) and ecosystem respiration ($Reco$). For days when the vegetation was photosynthetically active (i.e. days where there was a clear response of NEE to $PPFD$), total ecosystem respiration was calculated as the weighted average of nighttime respiration ($Reco_n$) and daytime respiration ($Reco_d$). Nighttime ($PPFD < 10$ μmol m^{-2} s^{-1}) CO_2 fluxes are assumed to represent ecosystem respiration at night. Daytime respiration was derived from the light response curves calculated for each day when the vegetation was photosynthetically active. The light response curve defines the relationship between CO_2 exchange during the day (NEE) and $PPFD$ ($PPFD > 10$ μmol m^{-2} s^{-1}), which can be described by a rectangular hyperbola (Gilmanov et al. 2003; Ruimy et al. 1995):

$$NEE = [(-F_\infty \times \alpha \times PPFD) / (\alpha \times PPFD + F_\infty)] + Reco_n \quad (2)$$

where F_∞ is NEE at light saturation (μmol m^{-2} s^{-1}), α is the apparent quantum yield, and $Reco_n$ (μmol m^{-2} s^{-1}) is to be interpreted as the best estimate of the average $Reco_d$ (Gilmanov et al. 2003; Suyker and Verma 2001).

GPP was then calculated as the difference between NEE and $Reco$. Therefore, negative values indicate CO_2 uptake by photosynthesis and positive values the release of CO_2 by respiration. For days without a clear response of NEE to $PPFD$, total ecosystem respiration was calculated from the exponential relationship between $Reco_n$ and soil temperature at -5 cm (°C) (Schmid et al. 2000),

$$Reco_n = a^{(b \times T_s)}, \quad (3)$$

where a and b are parameters determined by minimizing the sum of squares of the residuals and T_s (°C) represents the soil temperature at -5 cm.

The light-response approach was also used to fill gaps in our data to obtain annual and seasonal totals. Outside the growing season, however, fluxes did not show a clear dependency on $PPFD$ due to the lack of photosynthetic activity. Hence, gaps in the data had to be filled differently for the winter period: short gaps ($\leq$2 h) were filled by linear interpolation, while larger gaps were filled using the median flux value for each hour of the day, determined from available data 3 days prior and after the gap. Gap-filled data only served the purpose to obtain annual and seasonal budgets, but were not used to find relationships between snow cover and CO_2 flux.

Results

Snow cover

Snow coverage at Rigi Seebodenalp varied greatly among winters (Table 1; Fig. 2). During the years 2002/2003, 2003/2004 and 2004/2005 the site was snow covered during 88, 125 and 116 days. On average, Rigi Seebodenalp was snow covered during 30% of the year. Also the timing of the first (autumn) and the last (spring) day with snow cover was very variable during the three winter periods (Fig. 2). First snow in 2004 [day of year (DOY) 313; 9th November] blanketed the site 47 days later than in 2002 (DOY 266). In spring, the last snow melted much earlier in 2003 (DOY 102) compared to 2004 (DOY 130). Maximum snow depth was 70 cm.

Winter CO_2 fluxes

Daily CO_2 fluxes during the winter period (15th October–15th April) ranged from a net CO_2 uptake of -15.17 g C m^{-2} day^{-1} in spring 2005 (DOY 105) to a net CO_2 loss of 12.39 g C m^{-2} day^{-1} in February 2004 (DOY 51). The mean daily CO_2 fluxes (F; Table 1) varied substantially over the three winter periods, with moderate fluxes during 2002/2003 (2.09 ± 0.21 g C m^{-2} day^{-1}), largest values during 2003/2004 (3.39 ± 0.19 g C m^{-2} day^{-1}) and smallest fluxes during 2004/2005 (1.27 ± 0.25 g C m^{-2} day^{-1}).

A similar picture was given, when focusing on snow-covered days only, mean CO_2 losses (F_{snow}; Table 1) were remarkably higher in 2003/2004 (4.33 ± 0.18 g C m^{-2} day^{-1}) than during the two other winter periods (3.03 ± 0.31 g C m^{-2} day^{-1} in 2002/2003; 2.63 ± 0.17 g C m^{-2} day^{-1} in 2004/2005). This, together with the greater number of snow covered days (Dts; Table 1) in 2003/2004 (125 days) contributed substantially to the observation that the winter 2003/2004 had the highest mean daily CO_2 losses.

During snow free days in the winter period, mean daily net CO_2 fluxes fluctuated around zero with some days showing a net uptake but others showing a net carbon loss (Fig. 2). We distinguished between snow free days when there was no photosynthetic activity and thus daily gross primary production (GPP_d) ≥ -0.5 g C m^{-2} s^{-1} (F_{nsna}; Table 1) and

Table 1 Daily averages measured at Seebodenalp during three winter periods (183 days) from 15 October (day 288) until 15 April (day 105) in 2002–2003, 2003–2004 and 2004–2005 of soil temperature under snow cover at 5 and 30 cm depth for January–March (T_{s5}, T_{s30}), CO_2 flux (F), CO_2 flux over snow pack (F_{snow}), CO_2 flux without snow cover when GPP at noon ≥ -0.5 g C m^{-2} (F_{nsna}) and CO_2 flux without snow cover when GPP at noon < -0.5 g C m^{-2} (F_{nsa})

Period	T_{s5} (°C)	T_{s30} (°C)	F (g C m^{-2} day^{-1})	F_{snow} (g C m^{-2} day^{-1})	F_{nsna} (g C m^{-2} day^{-1})	F_{nsa} (g C m^{-2} day^{-1})	Ds (days)	Dts (days)	Df (day)	Dl (day)	Dgd (days)
2002/2003	0.88 ± 0.02	1.65 ± 0.08	2.09 ± 0.21	3.03 ± 0.31	3.32 ± 0.22	1.35 ± 0.22	73	88	266	102	26
2003/2004	1.20 ± 0.07	1.61 ± 0.09	3.39 ± 0.19	4.33 ± 0.18	3.22 ± 0.20	1.80 ± 0.22	111	125	278	130	18
2004/2005	0.41 ± 0.02	0.74 ± 0.05	1.27 ± 0.25	2.63 ± 0.17	1.75 ± 0.24	-0.78 ± 0.32	93	116	313	104	58

Ds is the number of days with snow coverage within the winter period, Dts is the number of total snow covered days for the three measurement years, Df and Dl are the days on which first (autumn) and last (spring) snow, respectively, occurred. Dgd is the number of growing days (mean air temperature >5°C)

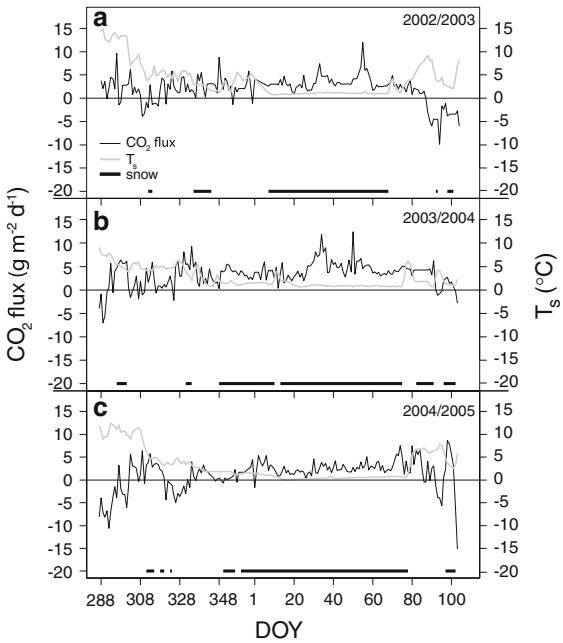

Fig. 2 Mean daily CO_2 fluxes (g C m^{-2} day^{-1}), mean soil temperature at −5 cm (°C, T_s) and snow cover presence (snow) during the three winter periods 2002/2003 (*a*), 2003/2004 (*b*) and 2004/2005 (*c*). Winter periods start at 15th October (day = 288) until 15th April (day = 105)

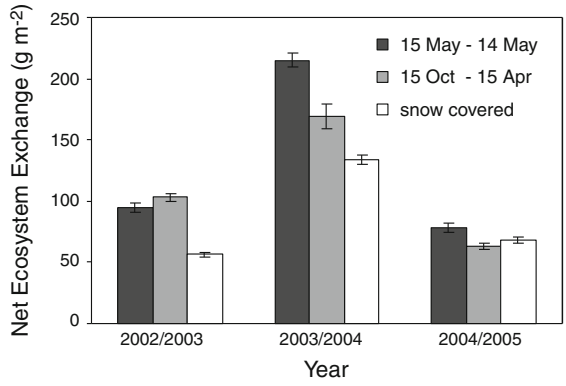

Fig. 3 *NEE* budgets (g C m^{-2}) at Rigi Seebodenalp, where a positive sign means a net loss. The annual *NEE* budget (calculated from 15th May until 14th May in the following year), the winter *NEE* budgets (calculated from 15th October until 15th April) and the *NEE* budget during snow covered periods were calculated for the three measurement years 2002/2003, 2003/2004 and 2004/2005

snow-free days where assimilation occurred and $GPP_d < -0.5$ g C m^{-2} s^{-1} (F_{nsa}; Table 1). CO_2 fluxes during snow free days without daily photosynthetic activity ≥ -0.5 g C m^{-2} s^{-1} (F_{nsna}) varied among the three winter periods between 1.75 ± 0.24 and 3.32 ± 0.22 g C m^{-2} day^{-1} (Table 1). Mean daily CO_2 exchange for snow-free days with photosynthetic activity (F_{nsa}) varied substantially. Net daily mean losses were measured in winter 2002/2003 (1.35 ± 0.22 g C m^{-2} day^{-1}) and in winter 2003/2004 (1.80 ± 0.22 g C m^{-2} day^{-1}). Contrastingly, a daily mean uptake was recorded in winter 2004/2005 (−0.78 ± 0.32 g C m^{-2} day^{-1}).

Annual CO_2 budgets, contribution of *NEE* and snow covered days

The interannual variability in CO_2 budgets was very high for the three winter periods (Fig. 3) and the annual CO_2 integrals (NEE_a; Table 2) demonstrate that the site was a net source of C during all years under observation. Over the winter period (NEE_w; Table 2) 2003/2004 the highest carbon loss was observed (169 ± 4 g C m^{-2}). Significantly lower losses were registered during the other winters (103 ± 3 g C m^{-2} in 2002/2003 and 63 ± 2 g C m^{-2} in 2004/2005). Still, the reported values show that winter emissions have a severe impact on the annual CO_2 budget. The share of carbon losses during snow covered days (NEE_s; Table 2) in 2002/2003 and 2004/2005 amounted to 56 ± 2 and 68 ± 2 g C m^{-2}, respectively. CO_2 efflux in 2003/2004 after the summer heat-wave in Europe (see Schär et al. 2004; Ciais et al. 2005) was twice as high (133 ± 4 g C m^{-2}).

When partitioning NEE into respiration and assimilation, it becomes clear that the highest contribution of snow covered periods ($Reco_s$; Table 2) to the annual ecosystem respiration was measured in 2003/2004. During these 2 years, $Reco_s$ contributed 6.5% to the total annual respiration ($Reco_a$; Table 2). The share of $Reco_s$ to $Reco_a$ was slightly lower in 2002/2003 (5.7%) and 2004/2005 (5.9%).

Highest NEE values measured during the winter period 2003/2004 (*F*; Table 1) are not the result of especially high winter respiration rates ($Reco_w$, Table 2), but are rather the result of intermediate respiration rates over the whole winter in combination with relatively low assimilation rates (GPP_w; Table 2) and the lowest number of growing degree days ($Dgd = 18$; Table 1). The share of ecosystem respiration measured during winter ($Reco_w$; Table 2) to the

Table 2 CO_2 budgets (g C m^{-2}) for the 3 years of measurements at Seebodenalp of net ecosystem exchange of CO_2 (*NEE*), of ecosystem respiration (*Reco*) and of gross primary production (*GPP*)

Year	NEE_a	NEE_w	NEE_s	$Reco_a$	$Reco_w$	$Reco_s$	GPP_a	GPP_w	GPP_s	$Reco_{w3}$
2002/2003	95 ± 4	103 ± 3	56 ± 2	1337 ± 19	374 ± 7	76 ± 3	−1242 ± 15	−274 ± 5	−15 ± 1	154 ± 5
2003/2004	215 ± 6	169 ± 4	133 ± 4	1602 ± 24	347 ± 7	140 ± 4	−1395 ± 18	−184 ± 3	−11 ± 2	150 ± 6
2004/2005	78 ± 5	63 ± 2	68 ± 2	1331 ± 20	269 ± 5	79 ± 2	−1256 ± 16	−208 ± 3	−13 ± 1	88 ± 4

The total annual budgets (suffix *a*), the budgets of CO_2 fluxes measured during winter from 15 October until 15 April (suffix *w*) and the budgets during snow cover (suffix *s*) are listed. $Reco_{W3}$ is the respiration budget for the 3 months winter period from 1st of December until 28th of February

total annual respiration ($Reco_a$; Table 2) varied between 28% (in 2002/2003) and 20% (in 2004/2005).

There was some photosynthetic activity during snow covered days that led to $GPP_s < 0$ (Table 2). Days with measurable assimilation only occurred towards the end of the snow period were both, snow-free and snow-covered patches were found within the footprint of the EC tower.

Environmental variables and CO_2 fluxes

In winter, air temperatures regularly dropped below 0°C. However, the soil at Rigi Seebodenalp never froze down to −5 cm (topsoil), where our near-surface soil temperature sensor was located, not even during snow free periods. Air-, snow-, and soil temperatures for a period with 40 cm snow cover in February–March 2005 were analyzed in detail (Fig. 4). Air temperatures at 2 m height were constantly below freezing. 10 cm above the snow (at 50 cm height) and in the snow pack (10 and 5 cm) temperatures were less negative and their peak values were slightly lagging air temperature. Temperature fluctuations in the air were strongly damped by the snow pack and were thus smallest near the soil. Below the snow cover, soil temperatures increased with depth (Fig. 5). The temperature of the first 50 cm of the soil under the snow pack (T_{s5}; Table 1) was higher in January–February 2004 than during the same months in the winter periods 2002/2003 and 2004/2005. Temperature in the uppermost soil layer (−5 cm) below the snow pack fluctuated between 0 and 2°C, but never dropped below 0°C.

In summer 2003, Europe experienced extremely hot temperatures (Schär and Jendritzky 2004; Luterbacher et al. 2004; Ciais et al. 2005). These high air temperatures in summer 2003 also translated into higher summer soil temperatures. However, the influence of this extreme event did not persist until the following winter. A cold snap in autumn 2003 (2nd October; day 273) reduced soil temperatures

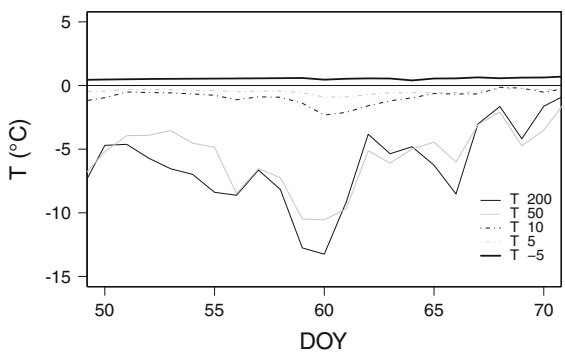

Fig. 4 Air (200, 50 cm), snow (10, 5 cm) and soil temperatures (−5 cm) for a period with 40 cm snow cover in February–March 2005 (days 50–70). Temperature fluctuations were damped from the free atmosphere over the snow towards the soil. The 0°C line is added to the graph

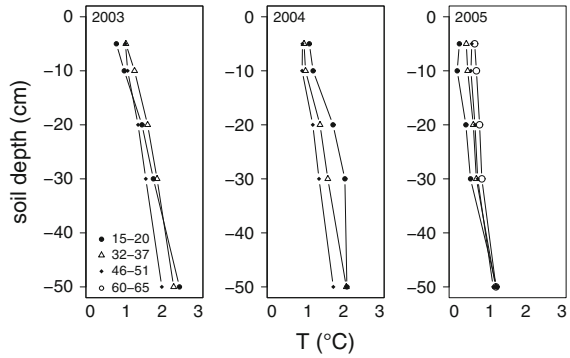

Fig. 5 Soil temperature profiles (°C) for four time intervals in spring 2002, 2003 and 2004. The four intervals are snow covered periods within the period 20 January (day 20)–10 March (day 69). Before day 20, there was at least 5 days of continuous snow cover in all winters

considerably, resulting in lower mean values in autumn 2003 compared to 2002 and 2004.

Since the temperature of the uppermost soil layer under snow cover fluctuated in the range 0–2°C, we hypothesized a constant CO_2 efflux from snow cover. However, considerable fluctuations in respiratory losses were measured over the snow pack (Fig. 2). We investigated the relationship between respiratory losses from snow covered grassland and meteorological variables such as snow depth, rate of snow melt, wind speed (Fig. 6), soil temperature (not shown) and air pressure (not shown). None of these variables explained more than 10% of the total variance in CO_2 efflux during periods with snow cover.

A more significant relationship was however found between snowmelt rates and CO_2 fluxes whenever snow had lasted for a duration of at least 7 days (Fig. 7). The diurnal patterns of the CO_2 flux (*NEE*) and soil temperature (T_s) are best illustrated by the interquartile range (the range between the 75%-quantile and the 25%-quantile of the 30-min fluxes of each day), which we denote as ΔNEE and ΔT_s, respectively (Fig. 7a–c). As long as the vegetation is inactive, we expect the interquartile range of *NEE* to be close to zero, thus no relevant diurnal course is expected. Similarly, ΔT_s is expected to be close to zero whenever the ground is snow covered or frozen, due to the fact that the phase change when melting or freezing water at temperatures close to 0°C consumes or produces heat and thereby reducing the daily amplitude of soil temperature fluctuations (Fig. 7, days before day 0). To separate conditions with inactive vegetation from such where it should be active, we used threshold values of 1.5 μmol CO_2 m^{-2} s^{-1} for ΔNEE and 0.5 K for ΔT_s.

As soon as the snow pack had disappeared, T_s immediately increased and a diurnal pattern ($\Delta T_s > 0.5$ K) was observed (Fig. 7a–c, days after day 0). The increase in T_s was correlated with the increase in photosynthetic activity, which was reflected in ΔNEE and in a decrease in *GPP*. However, the start of assimilation (*GPP*, negative values) and of the measured diurnal pattern of *NEE* did not coincide precisely with the time of snowmelt or the start of a measurable diurnal cycle in soil temperature (Fig. 7a, c). In 2004, photosynthetic activity was even observed 3 days before the diurnal pattern in soil temperature was detectable, which can be explained by the spatial heterogeneity of the snow pack during the period of snow melt (Fig. 7b).

In spring 2004, a clear increase in soil temperature was observed after snow had disappeared, and a net CO_2 uptake ($NEE < 0$) was measured from the very first day after snow melt (Fig. 7b). In 2003, it took 19 days from the time when snow had melted near the tower until a daily mean uptake was registered. Immediately after snow melt, changes in mean daily *NEE* were less pronounced than changes in ΔT_s.

Photosynthetic activity in spring

The photosynthetic rates in spring after day 104 (i.e. day of snowmelt in 2004) were similar during

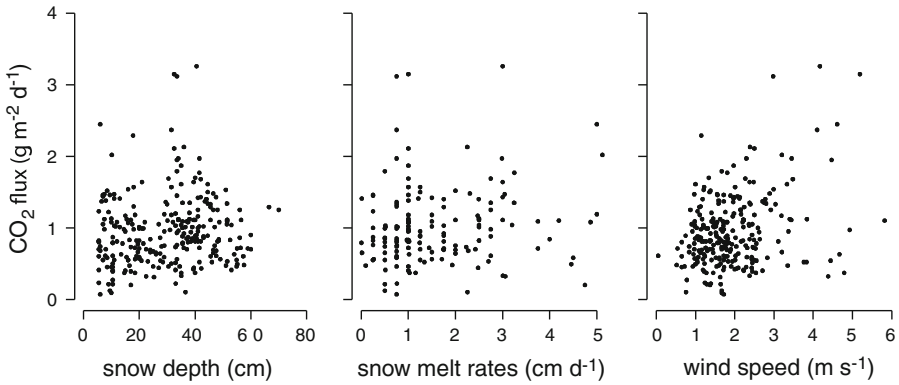

Fig. 6 Relationship between net daily CO_2 efflux (g C m^2 day^{-1}) from snow pack and snow depth, snow melt rates, and wind speed for snow covered days at Seebodenalp. None of the relationships explained more than 10% of the variance and we could thus not determine any statistically significant relationship between CO_2 efflux and the micrometeorological variables

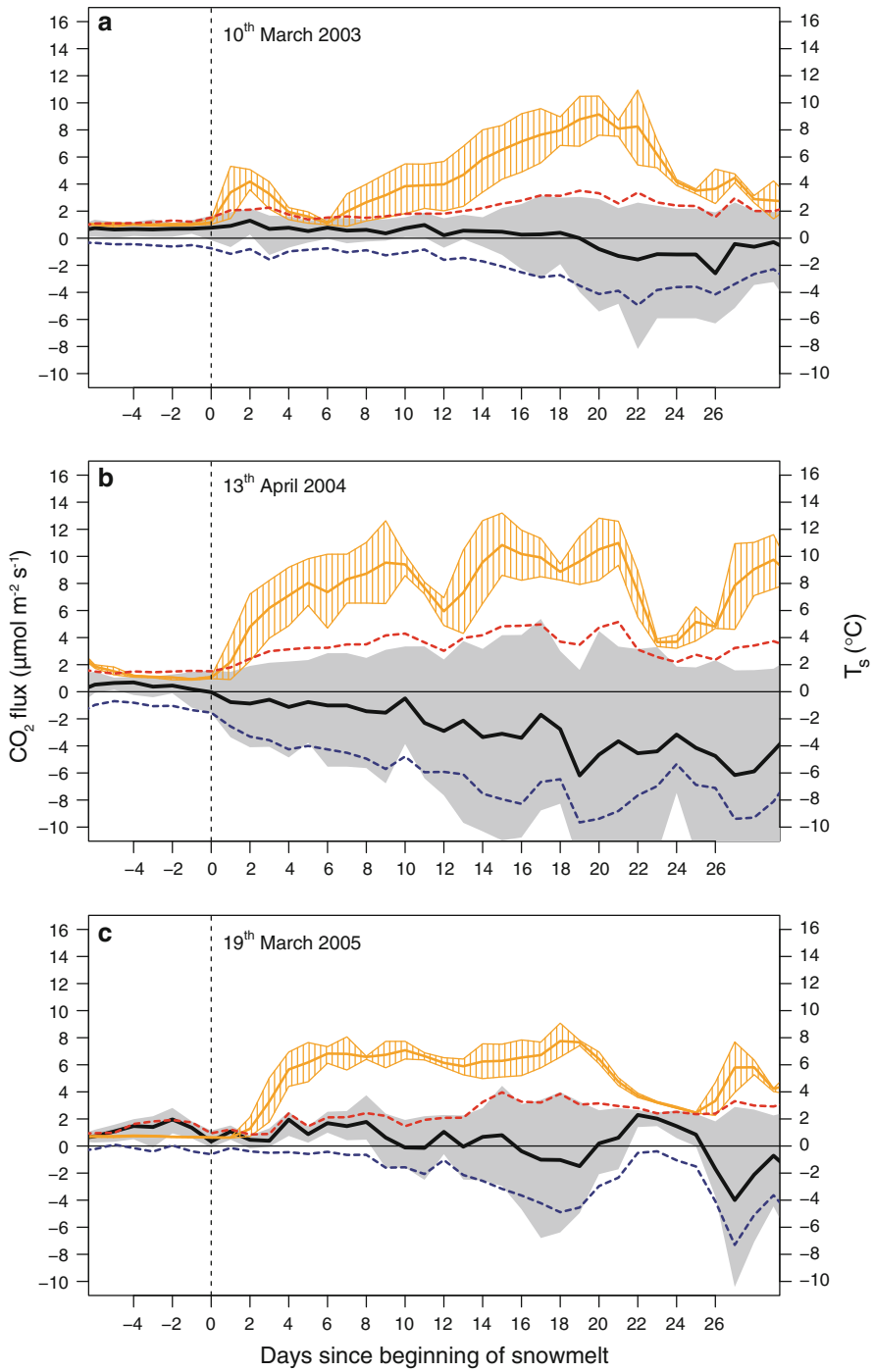

Fig. 7 Daily means of net CO_2 flux (*NEE*; µmol CO_2 m^{-2} s^{-1}), ecosystem respiration (*Reco*), gross primary production (*GPP*) and soil temperature (T_s; °C) at the beginning of spring (complete snow melt at day = 0) for the three winter periods 2002/2003, 2003/2004, and 2004/2005. The diurnal patterns of *NEE* (*black solid line*) and T_s (*orange solid line*) are visualized by the polygon areas covering the range between the 25 and 75% quantiles of *NEE* and T_s

the 3 years (Fig. 8). After maximum carbon losses in spring and before the first grass cut at the beginning of June, the slopes of the integrated assimilation fluxes (*GPP*) had similar steepness, indicating that the increment in net daily CO_2 flux is rather constant for the 3 years and hence largely unrelated to snow conditions of the previous winter.

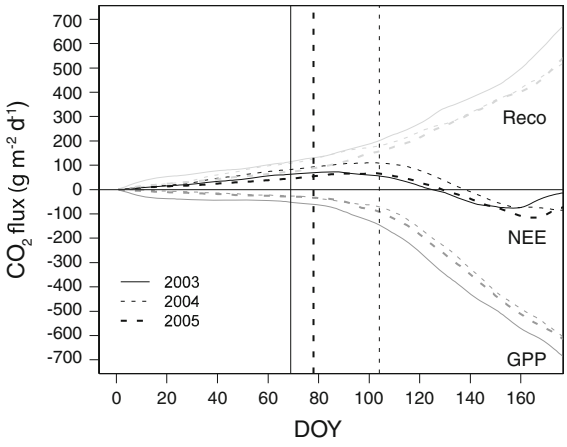

Fig. 8 Cumulative carbon fluxes of net CO_2 flux (*NEE*), of the respiration (*Reco*) and the assimilation (*GPP*) fluxes at Rigi Seebodenalp in spring 2003, 2004, and 2005. CO_2 integrals were calculated by integrating the CO_2 flux data from 1 January (day = 1). A positive sign means a net C loss. The *vertical lines* indicate the timing of the snow melt for each year

Discussion

Magnitude of CO_2 fluxes measured at Rigi Seebodenalp

The mean daily winter CO_2 efflux rates measured at Rigi Seebodenalp (Table 1) are situated in the upper range of available studies on respiration losses from seasonally snow covered non-forest ecosystems. Ham and Knapp (1998) reported average rates of wintertime CO_2 efflux of 0.95 g C m^{-2} day^{-1} measured at a tallgrass prairie and Volk and Niklaus (2002) detected respiratory losses of 1.2 g C m^{-2} day^{-1}. The high soil organic matter content at Rigi Seebodenalp (between 7.2 ± 0.2 and $15.7 \pm 0.9\%$ by mass) is certainly one of the relevant factors responsible for the high winter CO_2 efflux rates reported in this study. Average winter CO_2 respiration rates recorded in the arctic tundra are substantially lower than the values measured at Rigi Seebodenalp. Values for the arctic tundra are reported between 0.06 g C m^{-2} day^{-1} (Fahnestock et al. 1999) and 0.18 g C m^{-2} day^{-1} (Bubier et al. 2002). It appears that although arctic and alpine vegetation types are often considered to be similar, the presence (arctic) or absence of permafrost (below 2,580 m a.s.l. in the Alps; see Luetsch et al. 2004, 2004) are distinct differences for winter respiration rates.

Environmental variables and winter CO_2 fluxes

Winter CO_2 efflux is largely the result of microbial respiration, which is sensitive to soil temperature and soil moisture availability (Edwards and Cresser 1992; Liptzin et al. 2009; Schadt et al. 2003). Microbial activity increases exponentially with warmer soil temperatures (Mikan et al. 2002). The higher respiration rates under snow cover (F_s; Table 1) in 2003/2004 compared to the other two winters can thus be interpreted as the result of the higher soil temperatures (T_{s5}; Table 1). Deeper in the soil, the temperature was not significantly different between spring 2003 and spring 2004 due to cooling of this layer because of the constant soil heat flux towards the upper soil layer.

Liquid water, which is a prerequisite for cellular activity (Jones et al. 1999; Mikan et al. 2002), was available at Rigi Seebodenalp during winter and was favored by positive soil temperatures. The soil at Rigi Seebodenalp was never frozen down to −5 cm, neither during snow covered nor during snow free periods since snow cover effectively decouples soil temperatures from the atmosphere (Brooks et al. 2004) and keeps soils from deep-freezing due to insulation (Haebleri 1973; Hardy et al. 2001; Walker et al. 1999; Bubier et al. 2002; Shibistova et al. 2002; Swanson et al. 2005). But also during snow-free days with atmospheric frost, the soil at Rigi Seebodenalp did not freeze except for the topmost centimeters (≤5 cm) above our uppermost soil temperature sensor. Brooks et al. (1997) observed that in alpine tundra organic solutes act to suppress the freezing point in the organic soil horizon. The same observation was already described by Edwards and Cresser (1992), who found that a solute depression of the freezing point by ion diffusion as soils begin to freeze may result in thawed soils at temperatures below 0°C, which in combination with the geothermal heat flux due to the absence of permafrost is most likely responsible for the productive environmental conditions that the soil microorganisms experience in winter. Our measurements of soil temperature in the upper 50 cm of the soil indicate that heat, stored in the ground, is released in winter to keep snow basal temperatures close to 0°C (Haebleri 1973). This relation is only valid for systems without underlying permafrost. The temperature of the uppermost soil layer (−5 cm) below the snow pack fluctuated between 0 and 2°C, but never dropped below 0°C, as observed in mountainous areas

(Haebleri 1973). This does not mean that it is impossible that temperatures can drop below 0°C, and Sevanto et al. (2006) reported a short period where this general rule did not apply, probably caused by extremely dry and porous ground where cold air advection may have been responsible for temperatures as low as −4°C at 5 cm depth. However after roughly 3 weeks of snow cover this short-term deviation from the rule converged to the generally expected 0 to −1°C constant temperature in the mineral soil layer (Sevanto et al. 2006, their Fig. 1).

We were unable to determine any significant relationship between CO_2 efflux from the snowpack and micrometeorological variables such as soil temperature, snow depth, rate of snow melt, wind speed or air pressure. In the special case of soil temperature, the observed range of values under the snowpack was just too narrow (0–2°C) to describe CO_2 flux over snow pack as a function of soil temperature. This is in agreement with several other studies, which also did not find good correlations between the two variables (Nadelhoffer et al. 1991; Sommerfeld et al. 1993; Winston et al. 1997; Schmidt et al. 1999; Suni et al. 2003), although they were based on much wider soil temperature ranges. For tussock–tundra soils, Schimel and Clein (1996) found that there is generally very little response of soil respiration with temperatures below 10°C. Laboratory studies (Nadelhoffer et al. 1991) however indicate that there should be a strong relationship between soil temperatures and respiration even in frozen soils down to −10°C. Our data do not contradict this finding, but they clearly show that the observed range in soil temperatures under natural conditions do not allow to establish such a relationship.

Additionally, we could not find a clear effect of snow depth on CO_2 efflux, which is in agreement with the findings by Jones et al. (1999). In contrast, other authors (e.g. Welker et al. 2000; Gilmanov et al. 2004) determined a positive effect of snow depth on CO_2 efflux. Gilmanov et al. (2004), summarizes two opposing effects of snow cover on CO_2 exchange found in the literature: (1) depending on snow thickness and snow properties, snow cover can act as an almost impermeable coat and can thus significantly decrease the efflux of CO_2 to the atmosphere (Kelley et al. 1968); but (2) a thicker snow cover insulates the soil better and can create a more favorable environment for belowground respiration during winter (Welker et al. 2000; Liptzin et al. 2009).

Winter CO_2 budgets

The marginal CO_2 uptake in the winter of 2004/2005 could be explained by an extended autumn with photosynthetic uptake, and an earlier start of the growing season. In combination, this partially explained the relatively small daily mean loss determined over the whole winter period 2004/2005. The other important component that led to these small losses was that the winter period 2004/2005 was characterized by the highest number of growing degree days as similarly shown in a synthesis paper by Wang et al. (2011).

During the snow covered periods in 2003/2004 higher carbon losses were measured compared to the other two winter periods (Tables 1, 2). The higher temperatures of the topmost soil (T_{s5}; Table 1) are partially responsible for these differences (e.g. Reichstein et al. 2003, 2005). Another possible explanation for the high carbon losses measured during the winter following the summer heat-wave 2003 could be the flush of decomposition occurring after rewetting a dry soil (Franzluebbers et al. 2000). During the hot summer 2003 there were some periods where the vegetation at Rigi Seebodenalp suffered from water shortage. Due to water stress, a part of the soil microbial biomass and the roots died and this material is respired when the soil is rewetted. The process of drying and rewetting the soil generally results in an increment of the amount of available substrate, which forms the feeding basis for microbial respiration.

However, we could not detect the CO_2 flush following snow melt/rewetting as proposed by Franzluebbers et al. (2000, Figs. 7, 8), from the melting snow pack nor from the thawing of the soil or a larger availability of nutrient, which clearly differs from previous findings described in literature (e.g. Skogland et al. 1988; Panikov and Dedysh 2000; Prieme and Christensen 2001; Bubier et al. 2002). At Rigi Seebodenalp, there were several snow-melting events during the three winter periods (Fig. 2), the soil was never frozen and thus no freeze–thaw cycles were observed as reported in Liptzin et al. (2009). From this we conclude that we have a unique dataset that illustrates how environmental conditions in the Alps

differ from published knowledge with respect to winter CO_2 effluxes.

Definition of winter

As noted before, we chose a special definition for "winter" to match the true pattern of snow cover as well as possible. In this paper, we defined the winter season as the period from 15th October until 15th April. If we were to use another definition for winter, e.g. only the calendar months December, January, and February, winter CO_2 losses would only account for 11.5, 9.5, and 6.5% of the respective annual CO_2 budgets during the three years under observation (May–April). This definition would lead to a serious underestimation of the importance of winter conditions (characterized by snow cover at our location) in the annual balance. Irrespective of the definition of winter, we found that the snow and frost-free days at both the beginning and ending of the cold season can contribute considerably to the high interannual variability of mean daily fluxes and thus of the winter and growing season carbon budgets. Other studies also had to adopt the definition of winter to their locality (Oechel et al. 1997; Mast et al. 1998; Hobbie et al. 2000; Panikov and Dedysh 2000; Lafleur et al. 2001; Wickland et al. 2001; Hirano 2005; Wang et al. 2011). Therefore, a comparison with literature values not only depends on ecosystem properties, but also on the length of the winter season and micrometeorological conditions. The reason for this is related to the general issue of extensive versus intensive variables (see Legendre and Legendre 1998): winter respiration is an extensive variable "whose values, in a homogeneous system, changes proportionally (linear relationship) to the size of the sampling unit (transect, quadrat, or volume [in our case: length of time period])" (Legendre and Legendre 1998). Comparable estimates of winter respiratory losses fluctuate between 3 and 50% of the annual respiratory CO_2 losses for northern wetlands, arctic tundra (Oechel et al. 1997; Hobbie et al. 2000; Panikov and Dedysh 2000; Lafleur et al. 2001; Hirano 2005) and 10–20% in alpine and subalpine ecosystems (Mast et al. 1998; Wickland et al. 2001).

A special assessment on the definition of winter and how the corresponding values were affected, was published by Bubier et al. (2002). They demonstrated that the contribution of winter respiration to the total annual respiration varied between 3 and 25%, depending on the winter period definition.

Conclusions

Substantial amounts of CO_2 losses were observed at the sub-alpine Swiss CARBOMONT site Rigi Seebodenalp during three winter periods (integrated from 15th October until 15th April). Total winter respiration and respiration from snow pack contributed 23.3 ± 2.4 and 6.0 ± 0.3%, respectively, to the annual respiration losses at our research site. These winter carbon losses account for an important share in the annual CO_2 budgets, which emphasizes the importance of quantifying CO_2 fluxes outside the growing season.

Mean daily CO_2 fluxes in winter ranged from a net uptake to a net loss. The variability in winter fluxes was strongly determined by the CO_2 losses from snow pack, and by the micrometeorological conditions whenever there was no snow. Especially the days at the beginning and the end of the cold season had a strong influence on the seasonal budget, which therefore should be included in the definition of "winter" at our and comparable locations. The highest daily mean losses were recorded in winter 2003/2004. This is the combined result of: (1) the high respiration from the snowpack ($F_s = 4.33 \pm 0.18$ g C m^{-2} day^{-1}); (2) the long persistence of snow cover (111 days); and (3) the relatively low photosynthetic activity ($GPP_w = 184 \pm 3$ g C m^{-2}). Although the winter 2003/2004, which followed the European summer heat-wave 2003 had twice the respiration of the two other winters, we did not find sufficient evidence to attribute this to the special conditions observed during the heat-wave. This may be a result of the functional difference of grassland ecosystems when compared to forest ecosystems (Ciais et al. 2005) because of the much shorter C turnover time in grasslands as compared to forests, a fact needing further scientific attention. CO_2 exchange over grasslands in Europe has not been investigated as long as the various forest ecosystems analysed by Ciais et al. (2005). Therefore it would be too early to generalize our findings to other grassland ecosystems in Europe.

With reference to climatic changes it is noteworthy that the grassland ecosystem at Rigi Seebodenalp was ready to assimilate even during the winter whenever the snow cover had disappeared. Thus, our data

suggest that any changes in duration of the winter snow covers are expected to have a strong impact on the annual CO_2 budget, even if near-surface temperatures do not change considerably.

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References

Aubinet M, Grelle A, Ibrom A, Rannik Ü, Moncrieff J, Foken T, Kowalski AS, Martin PH, Berbigier P, Bernhofer Ch, Clement R, Elbers J, Granier A, Grünwald T, Morgenstern K, Pilegaard C, Rebmann C, Snijders W, Valentini R, Vesala T (2000) Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Adv Ecol Res 30:113–175

Aurela M, Laurila T, Tuovinen JP (2004) The timing of snow melt controls the annual CO_2 balance in a subarctic fen. Geophys Res Lett 31(16):4

Aurela M, Lohila A, Tuovinen JP, Hatakka J, Riutta T, Laurila T (2009) Carbon dioxide exchange on a northern boreal fen. Boreal Environ Res 14(4):699–710

Baldocchi DD (2008) Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. Aust J Bot 56:1–26

Baldocchi DD, Bowling DR (2003) Modelling the discrimination of $13CO_2$ above and within a temperate broad-leaved forest canopy on hourly and seasonal time scales. Plant Cell Environ 26(2):231–244

Baldocchi DD, Falge E, Gu LH, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer C, Davis K, Evans R, Fuentes J, Goldstein A, Katul G, Law B, Lee XH, Malhi Y, Meyers T, Munger W, Oechel W, KTP U, Pilegaard K, Schmid HP, Valentini R, Verma S, Vesala T, Wilson K, Wofsy S (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bull Am Meteorol Soc 82(11):2415–2434

Brooks PD, Schmidt SK, Williams MW (1997) Winter production of CO_2 and N_2O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. Oecologia 110(3):403–413

Brooks PD, McKnight D, Elder K (2004) Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. Glob Change Biol 11:231–238

Bubier J, Crill P, Mosedale A (2002) Net ecosystem CO_2 exchange measured by autochambers during the snow-covered season at a temperate peatland. Hydrol Process 16(18):3667–3682

Cernusca A, Bahn M, Berninger F, Tappeiner U, Wohlfahrt G (2008) Effects of land-use changes on sources, sinks and fluxes of carbon in European mountain grasslands. Ecosystems 11(8):1335–1337. doi:10.1007/s10021-008-9202-8

Christensen TR, Friborg T, Sommerkorn M, Kaplan J, Illeris L, Soegaard H, Nordstroem C, Jonasson S (2000) Trace gas exchange in a high-arctic valley 1. Variations in CO_2 and CH_4 flux between tundra vegetation types. Glob Biogeochem Cycles 14(3):701–713

Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437(7058):529–533

Edwards AC, Cresser MS (1992) Freezing and its effect on chemical and biological properties of soil. In: Stewart BA (ed) Advances in soil science, vol 18. Springer, New York, pp 59–79

Eugster W, Senn W (1995) A cospectral correction model for measurement of turbulent NO_2 flux. Boundary-Layer Meteorol 74(4):321–340

Fahnestock JT, Jones MH, Welker JM (1999) Wintertime CO_2 efflux from arctic soils: implications for annual carbon budgets. Glob Biogeochem Cycles 13(3):775–779

Flanagan LB, Wever LA, Carlson PJ (2002) Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Glob Change Biol 8(7):599–615

Frank AB, Dugas WA (2001) Carbon dioxide fluxes over a northern, semiarid, mixed-grass prairie. Agric For Meteorol 108(4):317–326

Franzluebbers AJ, Haney RL et al (2000) Flush of carbon dioxide following rewetting of dried soil relates to active organic pools. Soil Sci Soc Am J 64(2):613–623

Gilmanov TG, Johnson DA, Saliendra NZ (2003) Growing season CO_2 fluxes in a sagebrush-steppe ecosystem in Idaho: bowen ratio/energy balance measurements and modeling. Basic Appl Ecol 4(2):167–183

Gilmanov TG, Johnson DA, Saliendra NZ, Svejcar TJ, Angell RF, Clawson KL (2004) Winter CO_2 fluxes above sagebrush-steppe ecosystems in Idaho and Oregon. Agric For Meteorol 126(1–2):73–88

Grogan P, Illeris L, Michelsen A, Jonasson S (2001) Respiration of recently-fixed plant carbon dominates mid-winter ecosystem CO_2 production in sub-arctic heath tundra. Clim Change 50(1–2):129–142

Haebleri W (1973) Die Basis-Temperatur der winterlichen Schneedecke als möglicher Indikator für die Verbreitung von Permafrost in den Alpen. Zietschrift für Gletscherkunde und Glazialgeologie XI(1–2):221–227

Ham JM, Knapp AK (1998) Fluxes of CO_2, water vapor and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source. Agric For Meteorol 89(1):1–14

Hardy JP, Groffman PM, Fitzhugh RD, Henry KS, Welman AT, Demers JD, Fahey TJ, Driscoll CT, Tierney GL, Nolan S (2001) Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. Biogeochemistry 56(2):151–174

Hirano T (2005) Seasonal and diurnal variations in topsoil and subsoil respiration under snowpack in a temperate deciduous forest. Glob Biogeochem Cycles 19:GB2011. doi:10.1029/2004GB002259

Hobbie SE, Schimel JP, Trumbore SE, Randerson JR (2000) Global Chang Biol 6:196–210. doi:10.1046/j.1365-2486.2000.06021.x

IPCC (2007) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. IPCC, Cambridge

Johnson PL, Kelley JJ (1970) Dynamics of carbon dioxide and productivity in an arctic biosphere. Ecology 51(1):51:73–80. doi:10.2307/1933600

Jones MH, Fahnestock JT, Walker DA, Walker MD, Welker JM (1998) Carbon dioxide fluxes in moist and dry arctic tundra during season: responses to increases in summer temperature and winter snow accumulation. Arct Alp Res 30(4):373–380

Jones MH, Fahnestock JT, Welker JM (1999) Early and late winter CO_2 efflux from arctic tundra in the Kuparuk River watershed, Alaska, USA. Arct Antarct Alp Res 31(2):187–190

Kelley JJ, Weaver DF, Smith BP (1968) Variation of carbon dioxide under snow in the arctic. Ecology 49(2):358–361

Kutzbach L, Wille C, Pfeiffer EM (2007) The exchange of carbon dioxide between wet arctic tundra and the atmosphere at the Lena River Delta, Northern Siberia. Biogeosciences 4(5):869–890. doi:10.5194/bg-4-869-2007

Lafleur PM, Humphreys ER (2008) Spring warming and carbon dioxide exchange over low arctic tundra in central Canada. Glob Change Biol 14(4):740–756

Lafleur PM, Roulet NT, Admiral SW (2001) Annual cycle of CO_2 exchange at a bog peatland. J Geophys Res Atmos 106(D3):3071–3081

Legendre P, Legendre L (1998) Numerical ecology. Developments in environmental modeling Nr.20 (2nd edn). Elsevier, Amsterdam

Li SG, Asanuma J, Eugster W, Kotani A, Liu JJ, Urano T, Oikawa T, Davaa G, Oyunbaatar D, Sugita M (2005) Net ecosystem carbon dioxide exchange over grazed steppe in central Mongolia. Glob Change Biol 11(11):1941–1955

Liptzin D, Williams MW, Helmig D, Seok B, Filippa G, Chowanski K, Hueber J (2009) Process-level controls on CO_2 fluxes from seasonally snow-covered subalpine meadow soil, Niwot Ridge, Colorado. Biogeochemistry 95:151–166. doi:10.1007/s10533-009-9303-2

Luetsch M, Stoeckli V, Lehning M, Haeberli W, Ammann W (2004) Temperatures in two boreholes at Fluela Pass, Eastern Swiss Alps: the effect of snow redistribution on permafrost distribution patterns in high mountain areas. Permafr Periglac Process 15(3):283–297

Luterbacher J, Dietrich D, Xoplaki E, Grosjean M, Wanner H (2004) European seasonal and annual temperature variability, trends, and extremes since 1500. Science 303(5663):1499–1503

Mariko S, Nishimura N, Mo WH, Matsui Y, Kibe T, Koizumi H (2000) Winter CO_2 flux from soil and snow surfaces in a cool-temperate deciduous forest, Japan. Ecol Res 15(4):363–372

Mast MA, Wickland KP, Striegl RT, Clow DW (1998) Winter fluxes of CO_2 and CH_4 from subalpine soils in Rocky Mountain National Park, Colorado. Glob Biogeochem Cycles 12(4):607–620. doi:10.1029/98GB02313

Mauder M, Foken T, Clement R, Elbers A, Eugster W, Grünwald T, Heusinkveld B, Kolle O (2008) Quality control of CarboEurope flux data. Part 2: inter-comparison of eddy-covariance software. Biogeosciences 5:451–462. doi:10.5194/bg-5-451-2008,2008

McMillen RT (1988) An eddy-correlation technique with extend applicability to non-simple terrain. Boundary-Layer Meteorol 43(3):231–245

Merbold L, Kutsch WL, Corradi C, Kolle O, Rebmann C, Stoy PC, Zimov SA, Schulze ED (2009) Artificial drainage and associated carbon fluxes (CO_2/CH_4) in a tundra ecosystem. Glob Change Biol 15(11):2599–2614

Mikan CJ, Schimel JP, Doyle AP (2002) Temperature controls of microbial respiration in arctic tundra soils above and below freezing. Soil Biol Biogeochem 34(11):1785–1795

Müller (2004) Bodenatmung auf der Seebodenalp während der Vegetationsperiode 2003. Master's thesis, Institute of Geography, University of Bern

Nadelhoffer KJ, Giblin AE et al (1991) Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72(1):242–253

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G, Grulke N (1993) Recent change of arctic tundra ecosystems from a net carbon-dioxide sink to a source. Nature 361(6412):520–523

Oechel WC, Vourlitis G, Hastings SJ (1997) Cold season CO_2 emission from arctic soils. Glob Biogeochem Cycles 11(2):163–172

Osterkamp TE, Romanovsky VE (1997) Freezing of the active layer on the coastal plain of the Alaskan Arctic. Permafr Periglac Process 8(1):23–44

Panikov NS, Dedysh SN (2000) Cold season CH_4 and CO_2 emission from boreal peat bogs (West Siberia): winter fluxes and thaw activation dynamics. Glob Biogeochem Cycles 14(4):1071–1080

Prieme A, Christensen S (2001) Natural perturbations, drying-wetting and freezing-thawing cycles, and the emissions of nitrous oxide, carbondioxide and methane from farmed organic soils. Soil Biol Biogeochem 33(15):2083–2091

Reichstein M, Rey A, Freibauer A et al (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. Glob Biogeochem Cycles 17:1104. doi:10.1029/2003GB002035

Reichstein M, Subke JA, Angeli AC, Tenhunen JD (2005) Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? Glob Change Biol 11:1754–1767

Reutlinger F (2004) Zusammensetzung und Produktivität der Weidevegetation am Standort Seebodenalp. Master's thesis, Institute of Plant Sciences, ETH Zürich

Rogiers N, Eugster W, Furger M, Siegwolf R (2005) Effect of land management on ecosystem carbon fluxes at a

subalpine grassland site in the Swiss Alps. Theor Appl Climatol 80(2–4):187–203
Rogiers N, Conen F, Furger M, Stöckli R, Eugster W (2008) Impact of past and present land-management on the C-balance of a grassland in the Swiss Alps. Glob Change Biol 14(11):2613–2625
Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1995) CO_2 fluxes over plant canopies and solar radiation: a review. In: Begon M, Fitter AH (eds) Advances in ecological research. Academic Press, New York, pp 1–68
Schadt CW, Martin AP, Lipson DA, Schmidt SK (2003) Seasonal dynamics of previously unknown fungal lineages in tundra soils. Science 301(5638):1359–1361
Schär C, Jendritzky G (2004) Hot news from summer 2003. Nature 432:559–560
Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger M, Appenzeller C (2004) The role of increasing temperature variability in European summer heat waves. Nature 427: 332–336
Schimel JP, Clein JS (1996) Microbial response to freeze-thaw cycles in tundra and taiga soils. Soil Biol Biochem 28(8):1061–1066
Schimel D, Kittel TGF, Running S, Monson R, Turnispeed AA, Anderson DE (2002) Carbon sequestration studied in western U.S. mountains. EOS Trans Am Geophys Union 83(40):445
Schmid HP, Grimmond CSB, Cropley F, Offerle B, Su HB (2000) Measurements of CO_2 and energy fluxes over a mixed hardwood forest in the mid-western United States. Agric For Meteorol 103(4):357–374
Schmidt DS, Schmidt RA, Dent JD (1999) Electrostatic force in blowing snow. Boundary-Layer Meteorol 93:29–45
Sevanto S, Suni T, Pumpanen J, Grönholm T, Kolari P, Nikinmaa E, Hari P, Vesala T (2006) Wintertime photosynthesis and water uptake in a boreal forest. Tree Physiol 26:749–757
Shibistova O, Lloyd J, Evgrafova S, Savushkina N, Zrazhevskaya G, Arneth A, Knohl A, Kolle O, Schulze ED (2002) Seasonal and spatial variability in soil CO_2 efflux rates for a central Siberian *Pinus sylvestris* forest. Tellus B Chem Phys Meteorol 54(5):552–567
Skogland T, Lomeland S, Goksoyr J (1988) Respiratory burst after freezing and thawing of soil: experiments with soil bacteria. Soil Biol Biogeochem 20(6):851–856
Sommerfeld RA, Mosier RA, Musselmann RC (1993) CO_2, CH_4, N_2O flux through a Wyoming snowpack and implications for global budgets. Nature 361(6408):140–142
Sommerfeld RA, Massman WJ, Musselman RC, Mosier AR (1996) Diffusional flux of CO_2 through snow: spatial and temporal variability among alpine-subalpine sites. Glob Biogeochem Cycles 10(3):473–482
Suni T, Rinne J, Reissell A, Altimir N, Keronen P, Rannik Ü, Dal Maso M, Kulmala M, Vesala T (2003) Long-term measurements of surface fluxes above a Scots pine forest in Hyytiälä, Southern Finland, 1996–2001. Boreal Environ Res 8(4):287–301
Suyker AE, Verma SB (2001) Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. Glob Change Biol 7(3):279–289
Swanson AL, Lefer BL, Stroud V, Atlas E (2005) Trace gas emissions through a winter snowpack in the subalpine ecosystem at Niwot Ridge, Colorado. Geophys Res Lett 32(3):5
Vogel A, Hantke R (1989) Rigi: Zur Geologie des Rigigebietes. Mitteilungen der Naturforschenende Gesellschaft (Luzern)
Volk M, Niklaus PA (2002) Respiratory carbon loss of calcareus grasslands in winter shows no effect of 4 years' CO_2 enrichment. Funct Ecol 16(2):162–166
Vourlitis GL, Oechel WC (1999) Eddy covariance measurements of CO_2 and energy fluxes of an Alaskan tussock tundra ecosystem. Ecology 80(2):686–701
Walker MD, Walker DA, Welker JM, Arft AM, Bardsley T, Brooks PD, Fahnestock JT, Jones MH, Losleben M, Parsons AN, Seastedt TR, Turner PL (1999) Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrol Process 13(14–15):2315–2330
Wang T, Ciais P, Piao SL, Ottlé C, Brender P, Maignan F, Arain A, Cescatti A, Gianelle D, Gough C, Gu L, Lafleur P, Laurila T, Marcolla B, Margolis H, Montagnani L, Moors E, Saigusa N, Vesala T, Wohlfahrt G, Koven C, Black A, Dellwik E, Don A, Hollinger D, Knohl A, Monson R, Munger J, Suyker A, Varlagin A, Verma S (2011) Controls on winter ecosystem respiration in temperate and boreal ecosystems. Biogeosciences 8:2009–2025. doi:10.5194/bg-8-2009-2011
Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water-vapor transfer. Q J R Meteorol Soc 106:85–100
Welker JM, Fahnestock JT, Jones MH (2000) Annual CO_2 flux in dry and moist arctic tundra: field responses to increases in summer temperatures and winter snow depth. Clim Change 44(1–2):139–150
Wickland KP, Striegl RG, Mast MA, Clow DW (2001) Carbon gas exchange at a southern Rocky Mountain wetland, 1996–1998. Glob Biogeochem Cycles 15(2):321–335
Winston GC, Sundquist ET, Stephens BB, Trumbore SE (1997) Winter CO_2 fluxes in a boreal forest. J Geophys res-Atmos 102:28795–28804. doi:10.1029/97JD01115
Zeeman MJ, Hiller R, Gilgen AK, Michna P, Plüss P, Buchmann N, Eugster W (2010) Management and climate impacts on net CO_2 fluxes and carbon budgets of three grasslands along an elevational gradient in Switzerland. Agric For Meteorol 150(4):519–530
Zhuang QL, Melillo JM, Sarofim MC, Kicklighter DW, McGuire AD, Felzer BS, Sokolov A, Prinn RG, Steudler PA, Hu SM (2006) CO_2 and CH_4 exchanges between land ecosystems and the atmosphere in northern high latitudes over the 21st century. Geophys Res Lett 33(17):L17403
Zimov SA, Semiletov IP, Davidov SP, Voropaev YV, Prosyannikov CF, Wong SC, Chan YH (1993) Wintertime CO_2 emission from soil of northeastern Siberia. Arctic 46:197–204
Zimov SA, Davydov SP, Zimova GM, Davydova AI, Schuur EAG, Dutta K, Chapin FS (2006) Permafrost carbon: stock and decomposability of a globally significant carbon pool. Geophys Res Lett 33(20):L20502